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The entomofauna of the Lower Permian fossil insect beds of Kansas and Oklahoma, USA

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ABSTRACT

The Lower Permian Wellington Formation fossil beds of mid-continent North America are known best for the famous Elmo, Kansas locality. The Elmo site has produced tens of thousands of specimens from which more than 150 species of insects have been described. Equally productive and more widespread geographically, but less well-known, are the Midco, Oklahoma beds located some 270 km south of Elmo. The Midco beds have also yielded tens of thousands of specimens, but the material has been less well studied, and only half as many species have been identified from there. Renewed attention has been given in recent years to both the geology and palaeontology of the Wellington Formation. The history of these insect beds is recounted and the insect faunal composition is briefly reviewed. There are nearly 200 species in 106 genera, 53 families and 21 orders. Sizes (as measured by mean forewing length) range from 1.9 mm to 330 mm, with a mean of 22 mm and a median of 12 mm. Ten of 13 species with fore wings greater than 50 mm in length are Protodonata. Most species are known from one or a few specimens (abundance ranges from 1 to just under 400 specimens per species). Of ten species for which 50 or more specimens are known, eight are Grylloblattida (and six of these Grylloblattida: Lemmatophorina), indicating that these taxa were either quite abundant or were preferentially preserved, or both. When reviewing the holotype/neotype specimens used to describe the Wellington Formation species, we find that 62% consist of fore wings, while 9% are complete specimens. However, when considering all known specimens, 48% of the species are known only by their fore wings, while 13% are now represented by complete specimens, indicating the importance of continued collecting and review of Wellington Formation insect fossils.

KEY WORDS: Kansas, Oklahoma, Elmo, Midco, Lower Permian, Artinskian, Wellington Formation, fossil insects.

INTRODUCTION

The Lower Permian Elmo, Kansas, North American locality (Artinskian Age) is an important Palaeozoic fossil insect *Konservat-Lagerstätt*. Approximately 150 species of insects have been described from these beds, which were discovered by E.H. Sellards in the early 1900's. The Elmo locality insect-bearing strata are found within the Wellington Formation, which extends south from Elmo another 270 km to the vicinity of the city of Perry, Oklahoma, where the Midco fossil insect beds occur in a number of outcrops. The Midco locality, discovered by G.O. Raasch in the late 1930's, nearly a half century after Elmo, is less well studied; only half as many species are known from this locality. In the area between the Elmo and Midco localities, the Wellington Formation is covered by quaternary loess and alluvium and is exposed only in a few isolated locations. As a result, the only significant fossil insect beds are those at Elmo and Midco. Altogether approximately 200 species are known from the mid-continent Wellington deposits of Kansas and Oklahoma.

Little work has been done on the Wellington Formation insect fossils since the last paper on them by Frank Carpenter in 1979. However recent workers have begun to

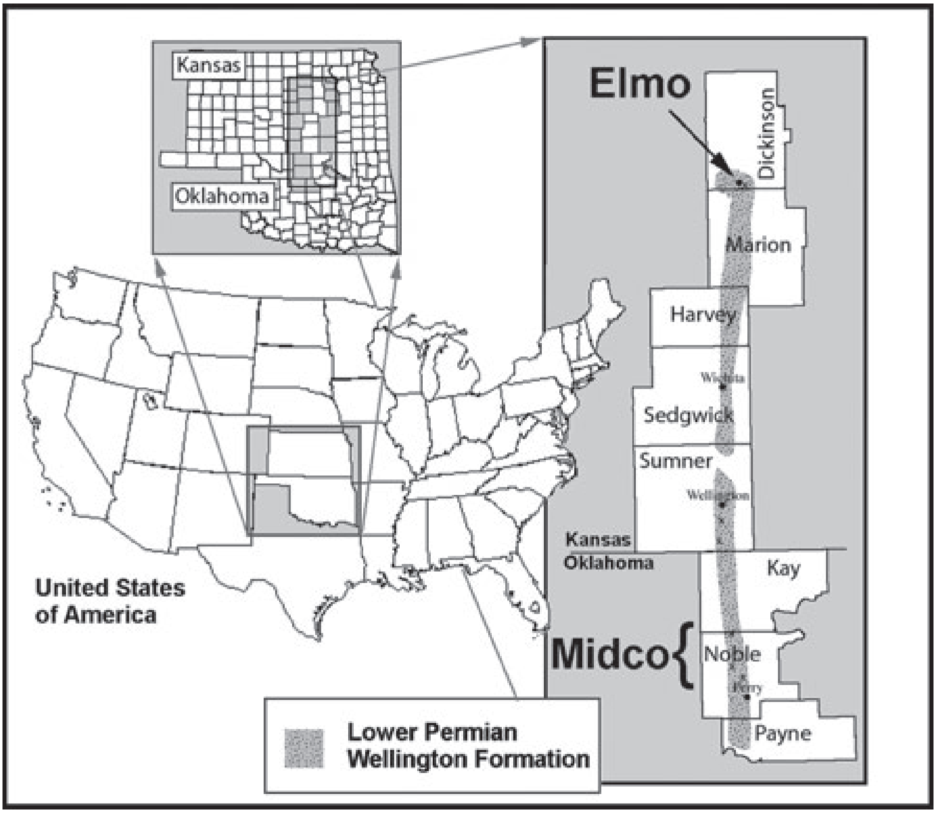
Kansas
Oklahoma
Elmo
Dickinson
Marion
Harvey
Wichita
Sedgwick
Sumner
Wellington
Kansas
Oklahoma
Kay
Midco
Noble
Perry
Payne
United States of America
Lower Permian Wellington Formation

Fig. 1. Location and extent of the North American mid-continent Lower Permian Wellington Formation insect fossil deposits. The formation runs north to south some 270 km along eight counties, with major sites at the northern (Elmo, Kansas) and southern (Midco, Oklahoma) extremities.

reinvestigate both the geology and palaeontology of the Wellington. In this paper we briefly describe the location and the history of exploration of these insect beds, after which we review the Wellington Formation entomofaunal taxonomic diversity and size ranges as measured by forewing lengths, specimen abundance, and specimen quality.

LOCATION AND EXTENT

The Wellington Formation occurs close to the geographic centre of the contiguous United States in North America. It extends from north-central Kansas south through north-central Oklahoma (Fig. 1). The insect-bearing deposits lie along what was, in Permian times, a coastal plain or marginal marine environment (Dunbar & Tillyard 1924; Carpenter 1947; Raasch 1946). The Elmo beds are considered to have been freshwater ponds or lakes while the Midco beds are thought to have been saline, possibly playa lakes (Carpenter 1947; Tasch 1964). Hall's (2004) recent reassessment of the Oklahoma Wellington Formation stratigraphy assigns the Midco beds to a marginal marine environment. The insects preserved as fossils are likely to have been allochthonous, and were either blown into the embayment by wind or washed into the embayment via streams (Hall 2004).

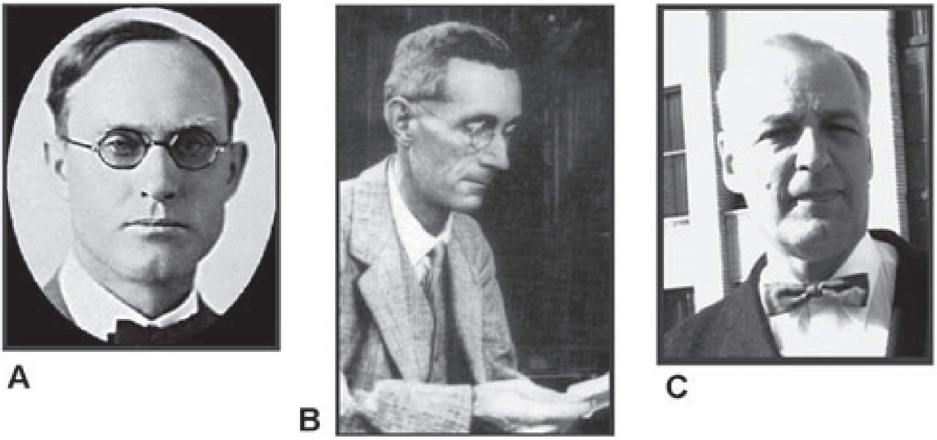

Fig. 2. (A) Elias H. Sellards (1875–1961) discovered the Elmo fossil beds (photo courtesy of the Texas Memorial Museum); (B) Robin J. Tillyard (1881–1937) studied Elmo fossils for a period of 16 years, carrying out his research in New Zealand and Australia. Eventually all the fossil specimens he worked with were returned to the Yale Peabody Museum (photo courtesy of the late Faith Tillyard Evans, Tillyard's daughter); (C) Frank M. Carpenter (1902–1994), of the Harvard Museum of Comparative Zoology and the dean of American palaeoentomologists, published definitive studies of the Elmo specimens over a period of some 60 years (photo courtesy of George Byers, University of Kansas).

HISTORICAL BACKGROUND

Elias H. Sellards (Fig. 2A) was studying Palaeozoic plant fossils under Samuel Williston at Kansas University in 1899 when he found two fossil insects among a collection of plant fossils from the Wellington Formation. He was interested enough to make trips to the locality, which was located near the small settlement of Elmo, Kansas (Fig. 3). He eventually collected some 2000 insect specimens. After completing a PhD at Yale University in 1903, he began a study of the Wellington Formation material, eventually describing many species, 27 of which are today recognized as valid. Sellards kept most of his specimens, but deposited a small representative collection in the Yale Peabody Museum.

In 1920, the distinguished entomologist Robin J. Tillyard (Fig. 2B), then residing in New Zealand and working at the Cawthron Institute in Nelson, was visiting Yale on a trip through the United States. He was excited to see a series of Sellards' fossil specimens in the Peabody Museum. His enthusiasm led Charles Schuchert and Carl Dunbar of Yale to obtain funding and embark on a collecting expedition to the Elmo beds. Another 2000 specimens were gathered. These were shipped to Tillyard in New Zealand, and he commenced a 16-year study of the material. Tillyard described 55 valid species of Elmo insects.

Frank M. Carpenter (Fig. 2C) began to work on Elmo fossil specimens in 1925. He published his last papers on them in the late 1970's. His prolific and definitive work on the Elmo fossils included revisions of taxa established by Sellards and Tillyard. Later, he also published on the Midco palaeopterous specimens (Carpenter 1947, 1979). Carpenter named a total of 96 valid species from Elmo and Midco.

E.B. Klots (1944) briefly discussed some protodonate and protozygopterous specimens from the Elmo beds, but did not describe any new species.

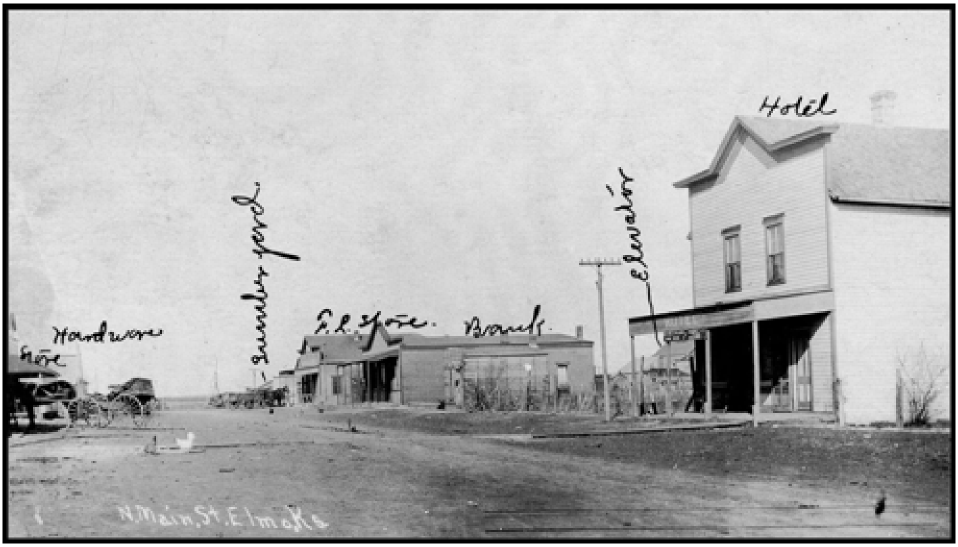

Fig. 3. The settlement of Elmo, Kansas, as it appeared in the early 1900's. The fossil beds, located a few miles southeast, were named after the town. (Photo courtesy of the Wichita State University Libraries Department of Special Collections.)

In the late 1930's, Gilbert O. Raasch (Fig. 4A) was working on a PhD in geology, studying the stratigraphy of the Wellington Formation in Oklahoma (Raasch 1946). He discovered a number of localities that were quite rich in fossil-insect material, and contacted Frank Carpenter. In 1940 the two men collected some 5000 specimens in ten weeks of field time. Subsequent collecting by Carpenter brought the total number of specimens from Midco in the Harvard Museum of Comparative Zoology collection to about 8000 (Carpenter 1979). Raasch eventually switched his interests to Cambrian trilobites of the Upper Mississippi Valley.

During the late 1950's and early 1960's, Paul Tasch (Fig. 4B), of Wichita State University, began working on the palaeolimnology of the Wellington Formation in Kansas and Oklahoma. He discovered insect fossils at a number of sites, and his associate, James Zimmerman, an entomologist from Wichita State University, eventually named eight species from the Oklahoma material (Tasch & Zimmerman 1962).

During the 1960's, Jarmila Kukalová-Peck studied a number of Wellington Formation taxa as part of her research on Palaeozoic insects. She reviewed the nymphal Ephemeroptera fossils collected by Carpenter from the Midco beds, determining them as the Wellington Formation genus *Protereisma*, but did not assign any specific names (Kukalová-Peck 1968). However, Demoulin, based solely on Kukalová-Peck's paper, assigned generic and specific names to her specimens in 1970. Hubbard and Kukalová-Peck (1980) and Carpenter (1979, 1992) eventually corrected Demoulin's work. The only valid Midco species named by Demoulin is *Protereisma americana* (Demoulin 1970).

A complete list of references to the Wellington Formation publications of the above researchers and a more detailed history of the Elmo locality have been published elsewhere (Beckemeyer 2000).

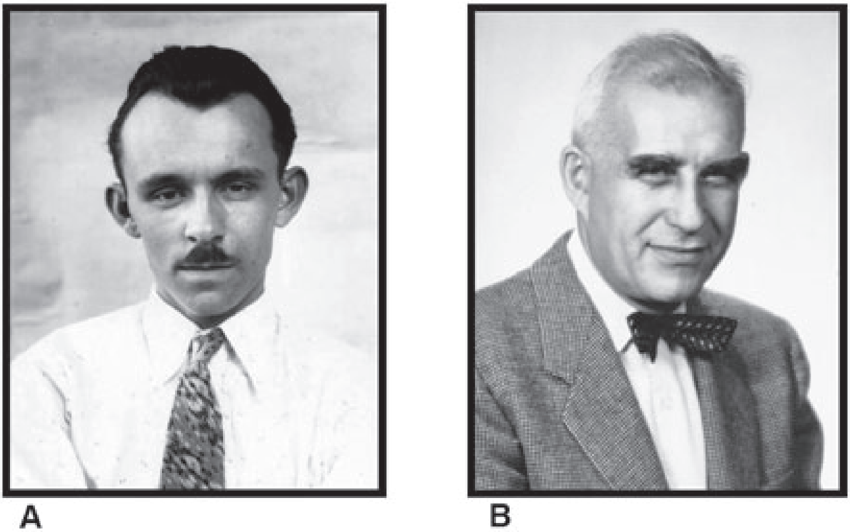

Fig. 4. (A) Gilbert O. Raasch (1903–1999) discovered the Midco fossil insect beds and documented the stratigraphy of the Oklahoma Wellington Formation in his PhD Thesis (Raasch 1946) (photo courtesy University of Wisconsin-Madison); (B) Paul Tasch of Wichita State University studied the palaeolimnology of the Wellington Formation in Kansas and Oklahoma and discovered additional Wellington Formation fossil insect localities in the late 1950's and early 1960's (photo courtesy of Wichita State University Department of Special Collections, Wichita, Kansas).

TABLE 1

Repositories of collections of Elmo and/or Midco Lower Permian Wellington Formation insect fossils.

Location	Collection Size/ Importance	Notes
Yale Peabody Museum	Major	Dunbar collection containing Tillyard's types
Harvard Museum of Comparative Zoology	Major	Carpenter's Elmo and Midco material: many thousands of specimens including types and large series
Texas Memorial Museum, University of Texas	Minor	Some of Sellards' type material
American Museum of Natural History	Minor	Klots protodonate and protozygoptera wings
University of Kansas Natural History Museum	Minor	Mostly Elmo material
Kansas State University Entomology Department	Minor	Some Elmo material including the Wenger-Holmes *Megatypus schucherti* counterpart
Oklahoma State University Entomology Department	Minor	Material from Midco
Wichita State University Geology Department	Minor	Some of Tasch's material, mostly from Midco, but with some Elmo material as well
Emporia State University	Minor	Mostly Midco material, comprised of the collections of the authors of this paper and including some type material

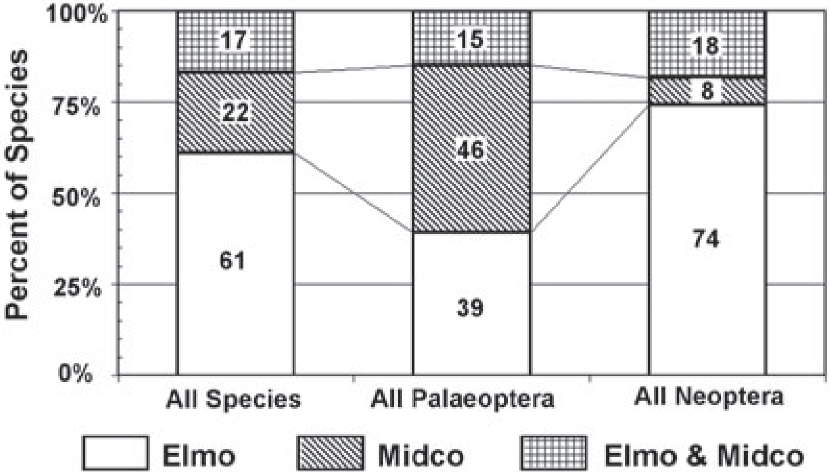

Fig. 5. Proportion of Wellington Formation entomofauna Neoptera and Palaeoptera subgroups unique to or shared between the Elmo and Midco localities, illustrating that the greater percentage of unique fauna at Elmo arises from the Neoptera. This reflects the fact that no review of the Neoptera from Midco has yet been published.

In recent times, beginning in the late 1990's, there has been renewed interest in the Wellington Formation entomofauana. Local workers, including Michael Engel of the University of Kansas and his students (Engel 1998; Lubkin & Engel 2005), and the authors (Beckemeyer 2000, 2004*a*, *b*, *c*; Beckemeyer & Byers 2001; Hall 2004) have started a fresh round of research. In addition, Béthoux *et al.* (2004) recently published a paper dealing with the order Caloneurodea from the Wellington Formation.

The Yale Peabody Museum and Harvard Museum of Comparative Zoology are the major repositories for the fossils, but there is a number of smaller collections (Table 1).

REVIEW OF THE ENTOMOFAUNA

Taxonomic diversity

A total of 194 valid insect species are currently known from the Wellington Formation; 118 (61%) are known only from Elmo, 43 (22%) are exclusive to Midco, and 33 (17%) are common to both localities. The lower number of species unique to Midco reflects the fact that Carpenter published only on the palaeopterous insects of Midco and not on the Neoptera (Fig. 5). Furthermore, there have been no reviews published or surveys conducted of Midco Neoptera. Since 1998, seven new Wellington Formation species have been described (Table 2) and seven species previously known from Elmo have been found to occur at Midco as well. Undoubtedly, many more species will be added upon a complete review of the neopterous material from Midco.

We compare the Elmo entomofauna distribution by major group (Holometabolous Neoptera, Paraneoptera, Polyneoptera, Palaeoptera, Apterygota) with the extant World insect fauna (figures for modern orders were taken from Grimaldi & Engel 2005) (Fig. 6). Insects with complete metamorphosis accounted for only about 7% of Elmo species, while today they are the most numerous of insects, accounting for approximately 83% of described species. Palaeoptera today account for less than 1% of the extant insect fauna while for Elmo, the group comprised nearly 27% of the species.

TABLE 2

New species added to the Wellington entomofauna since the publication of Carpenter's Treatise (1992).

Superorder	Order	Family	Genus	Species	Locality
Palaeoptera	Protodonata	Meganeuridae Handlirsch, 1906	*Megatypus* Tillyard, 1925	*parvus* Engel, 1998	Elmo
Neoptera	Caloneurodea	Uncertain Family	*Lipogramma* Béthoux *et al.*, 2004	*sinuosa* Béthoux *et al.*, 2004	Midco
Neoptera	Caloneurodea	Uncertain Family	*Gigagramma* Béthoux *et al.*, 2004	*carpenteri* Béthoux *et al.*, 2004	Midco
Neoptera	Grylloblattida: Protoperlina	Raaschiidae Beckemeyer, 2004	*Raaschia* Beckemeyer, 2004	*oklahomensis* Beckemeyer, 2004	Midco
Neoptera	Uncertain Order	Lophioneuridae Tillyard, 1921	*Cyphoneurodes* Bekker-Migdisova, 1953	*patriciae* Beckemeyer, 2004	Midco
Neoptera	Diaphanopterodea	Martynoviidae Tillyard, 1932	*Martynovia* Tillyard, 1932	*halli* Beckemeyer, 2004	Midco
Neoptera	Coleoptera	Uncertain Family	*Permocoleus* Lubkin & Engel, 2005	*wellingtonensis* Lubkin & Engel, 2005	Midco

Species diversity by major taxon (Order in most cases, Order: Suborder for the Grylloblattida) is shown for Elmo and Midco on Fig. 7. The ordinal system used is that of Carpenter (1992), with some modifications. Carpenter's "Protorthoptera" are placed in the Grylloblattida, Hypoperlida, and Blattinopseida, following Rasnitsyn and Quicke (2002). Classification of the Grylloblattida suborders follows Storozhenko (1998, 2002). Carpenter's Homoptera are grouped with the Hemiptera. The family Lophioneuridae is considered a stem group of Thysanoptera, after Kukalová-Peck (1991). The data are grouped into Apterygota, Pterygota: Palaeoptera and Pterygota: Neoptera sections, with the taxa arranged in each section in order of decreasing species diversity.

A nearly complete species list of Elmo insects may be found in Beckemeyer (2000). The Wellington entomofauna is quite diverse with 21 orders, 53 families and 106 genera represented.

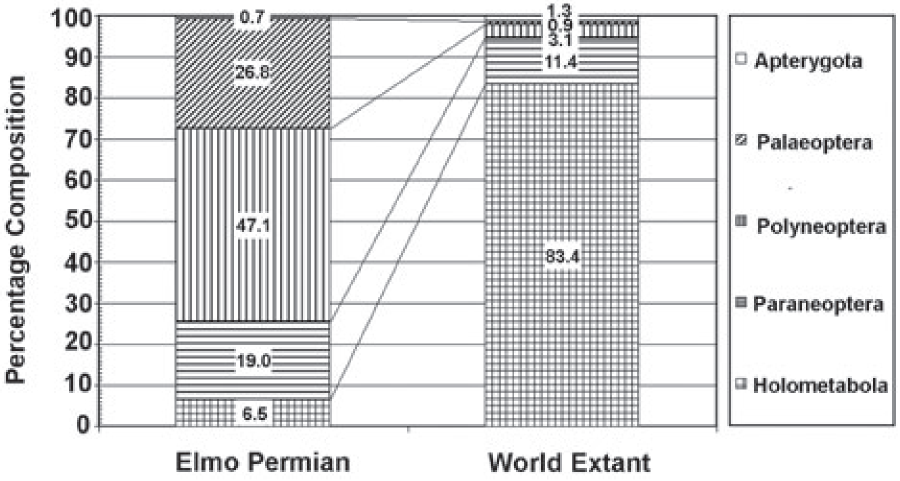

Fig. 6. Comparison of the distribution of the Elmo Permian and World extant entomofaunas by major groups: Apterygota, Palaeoptera, Polyneoptera, Paraneoptera, and Holometabola.

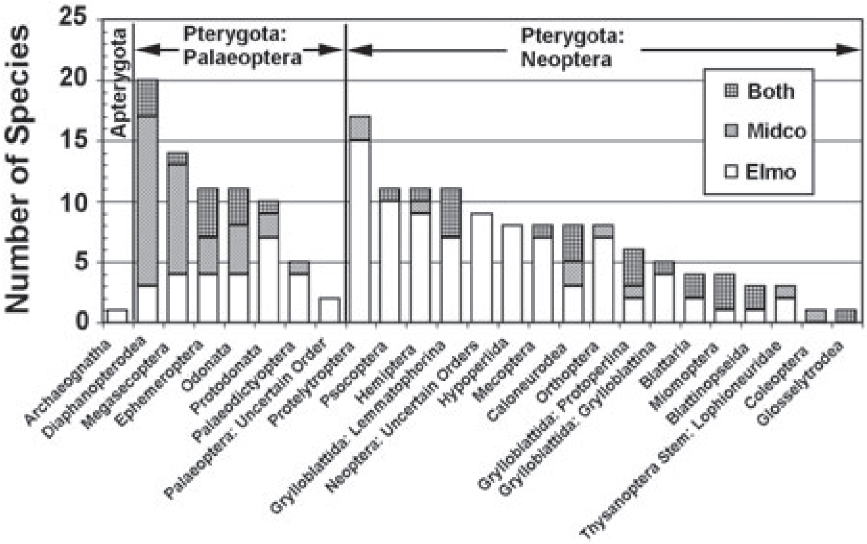

Fig. 7. Species diversity of the Wellington Formation entomofauna by Order (Suborder for the Grylloblattida). Orders are placed in three groups, Apterygota, Pterygota: Palaeoptera, and Pterygota: Neoptera, and are arranged in decreasing order of number of species. Bars show the number of species in each taxon unique to Elmo, unique to Midco and common to both. The nearly 200 species represent some 21 orders, 53 families and 106 genera.

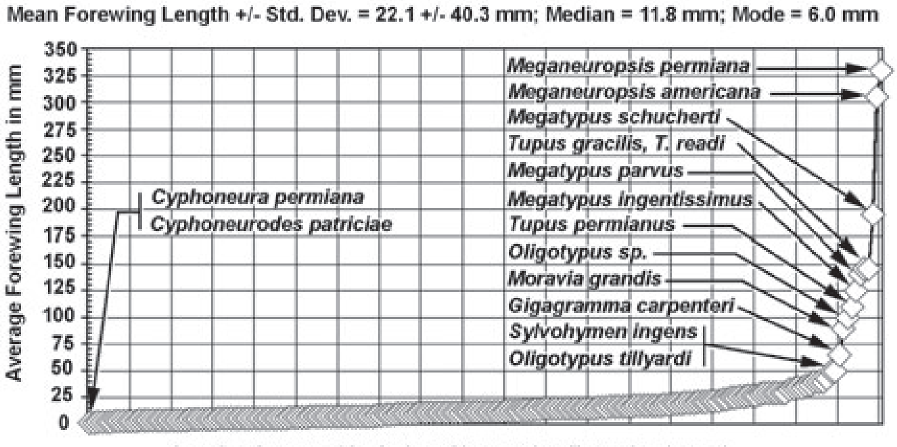

Fig. 8. Distribution of size in the Wellington Formation entomofauna. Size is based on average forewing length in mm, plotted from smallest species to largest species. The 13 largest (forewing length >100 mm) and 2 smallest (forewing length <2 mm) species are identified. The two smallest species are both in the family Lophioneuridae. Ten of the largest species belong to the order Protodonata; *M. grandis*, to Palaeodictyoptera; *G. carpenteri*, to Caloneurodea; and *S. ingens*, to Megasecoptera.

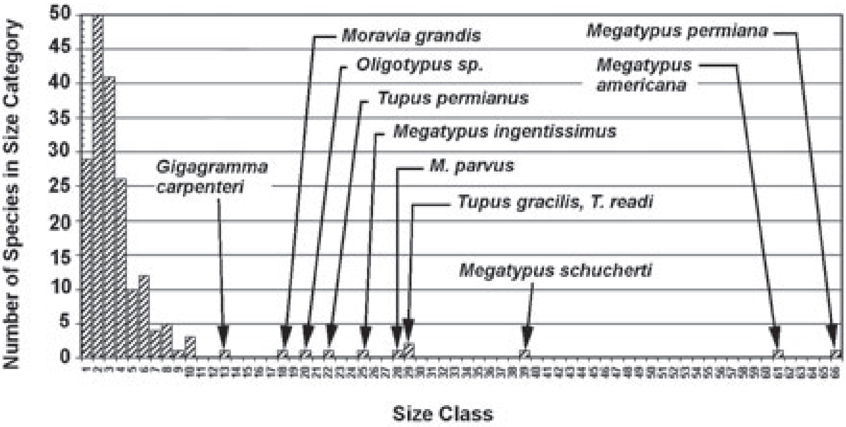

Fig. 9. Frequency distribution in 5-mm size classes of average forewing lengths for the Wellington Formation entomofauna.

Size diversity

The common view of Palaeozoic insects is that they were quite large, and, indeed, the largest insect known to have flown, the meganeurid *Meganeuropsis permiana* Carpenter, 1939, was described from the Elmo deposits. However, most of the insects of the Wellington formation were small, with fore wings less than 25 mm in length (Figs 8, 9). The mean length was 22 mm, the median 12 mm, and the mode 6 mm.

On Fig. 8, we have noted the species names of the insects with forewing lengths equal to or greater than 50 mm and those with forewing lengths less than or equal to 2 mm. Ten of the 13 insects with forewings of 50 mm or more were Protodonata. *Moravia grandis* is a palaeodictyopteran (Calvertiellidae), *Gigagramma carpenteri* is in the order Caloneurodea, and *Sylvohymen ingens* is in the order Megasecoptera. These are all extinct orders. The two species with the smallest forewings, 1.9 mm in length, are both in the Lophioneuridae, a family considered to be in a primitive stem group of the extant Thysanoptera.

Plotting forewing lengths in increasing size by taxon (order) (Fig. 10) gives an interesting observation that there is a fairly continuous gradation of size in most orders. This is even true of the Protodonata, a predatory order that contains most of the large species. However, in the three orders that contain a single large species (Palaeodictyoptera, Caloneurodea, and Megasecoptera), such species are the exception when compared to the majority of insects in these orders, which are much smaller and generally similar in size. It would be interesting to see analogous distributions for Carboniferous and Late Permian assemblages; one might anticipate a trend of decreasing size in these non-predatory groups from the Carboniferous, through the Lower Permian and into the Upper Permian, in response to selective predation by the large protodonates.

Specimen abundance

The number of adult specimens known per species in increasing order for the Elmo entomofauna is plotted in Fig. 11. The frequency distribution data for 10-specimen size classes are shown in Fig. 12. The mean is 21 specimens, but the median is 2 and the

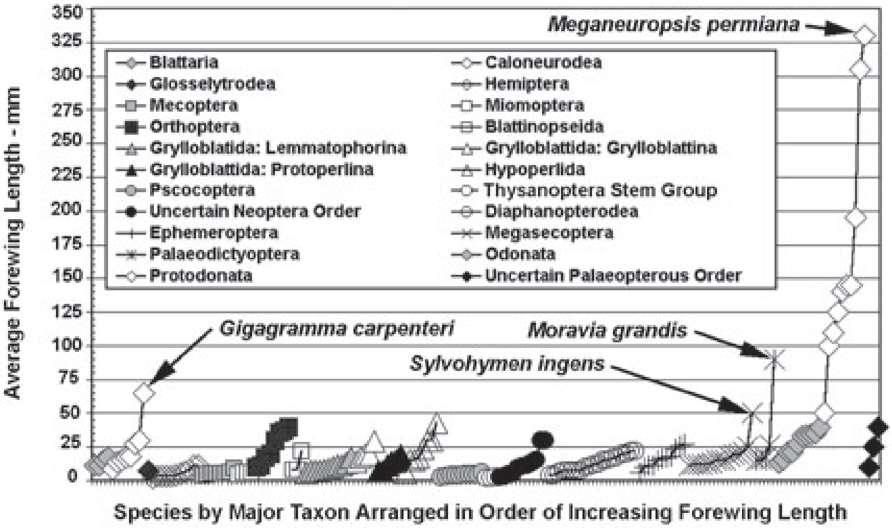

Fig. 10. Size distributions of the Wellington Formation entomofauna by major taxonomic groups. Size is based on average forewing length in mm.

mode 1. The high mean is due to half a dozen species for which large numbers of specimens have been found. Species for which more than a hundred specimens are known are identified in Figs 11 and 12. Of these six species, four (*Lemmatophora typa* Sellards, 1909, *Artinska clara* Sellards, 1909, *A. ovata* Sellards, 1909 and *Lisca minuta* Sellards, 1909) are Grylloblattida: Lemmatophorina: Lemmatophoridae. One species, *Probnis speciosa* Tillyard, 1939, belongs to Grylloblattida: Protoperlina: Probnidae,

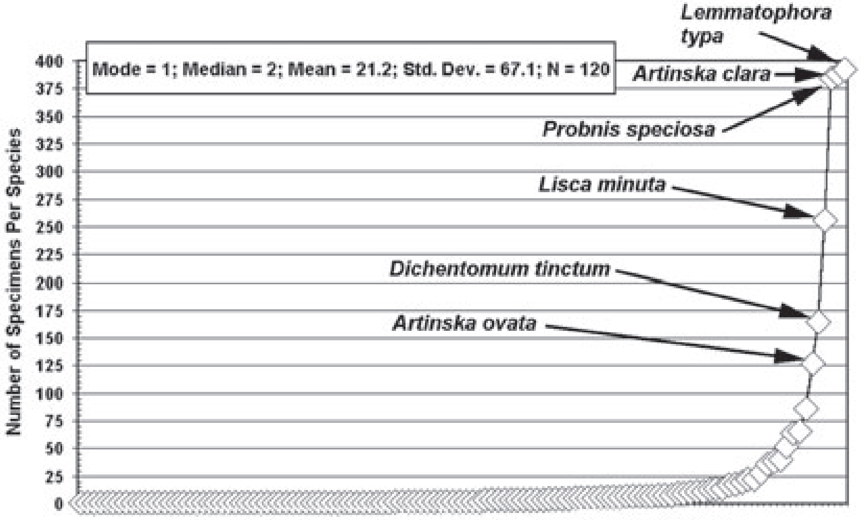

Fig. 11. Abundance of adult specimens of Elmo entomofauna. Values are plotted from species with fewest known specimens to species with the most known specimens. The species with the greatest numbers of specimens are identified. All labelled taxa are Grylloblattida except for *D. tinctum* (Psocoptera).

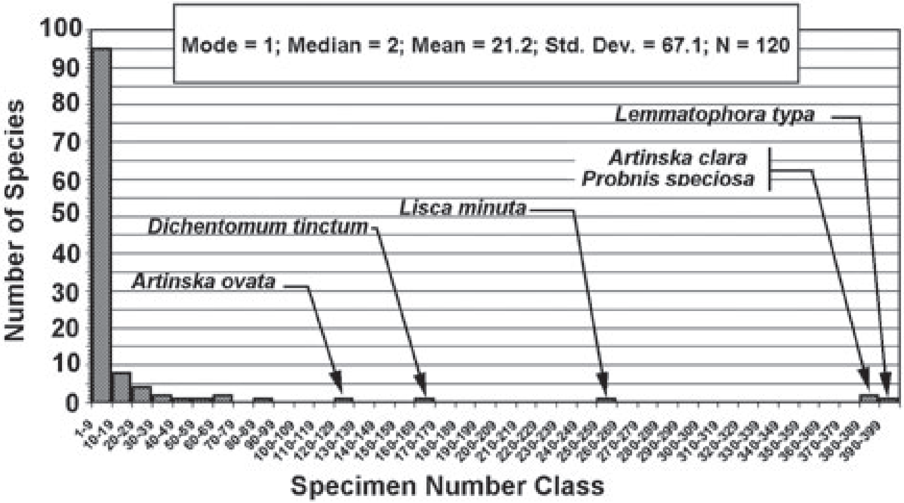

Fig. 12. Frequency distribution of adult-specimen abundance in 10-specimen size classes for the Elmo entomofauna.

and the last species, *Dichentomum tinctum* (Tillyard, 1926), is Psocoptera: Psocidiidae. Of the four species with more than 50 and less than 100 specimens, *Protereisma permianum* Sellards, 1907 (52 specimens) is Ephemeroptera: Protereismatidae, *Liomopterum ornatum* (Sellards, 1909) (86 specimens) is Grylloblattida: Grylloblattina: Liomopteridae, and the other two, *Lecorium elongatum* Sellards, 1909 and *Paraprisca fragilis* (Sellards, 1909), are lemmatophorids (66 and 64 specimens, respectively). Five of the six species with more than a hundred specimens and eight of the ten species with more than 50 specimens are Grylloblattida. Thus, the grylloblattids were either fairly abundant in the Elmo Permian, or they were preferentially preserved, or both.

Specimen abundance per species in increasing order of abundance by taxon is shown in Fig. 13. These taxa are plotted at the ordinal rank, except for the Grylloblattida, which are plotted at the Suborder rank. It is of interest to note that there is a relatively smooth distribution of abundance numbers for the Lemmatophorina, with nearly all the species in the family being well represented. For the other taxa which have species with a large number of specimens, most species in the relevant taxon have few specimens, and thus the well-represented species are exceptional. This can be seen in the Protoperlina, the Psocoptera, the Ephemeroptera, and several other groups. An interesting future study would be to determine if there are any obvious differences between the abundant and rarer species in these taxa that might account for their specimen numbers.

Nymphal vs. adult specimens

The great majority of the specimens from the Elmo locality are remains of adult insects. However, Carpenter (1935) reported 82 specimens of nymphs of which he determined to be at least two species of Lemmatophoridae, the family that is so well represented at Elmo by adult specimens. He based the separation of nymphal specimens on size, with nearly half being 9–10 mm in length and the other half 4.5–5.5 mm long. The larger specimens were considered by Carpenter (1992) most likely to be

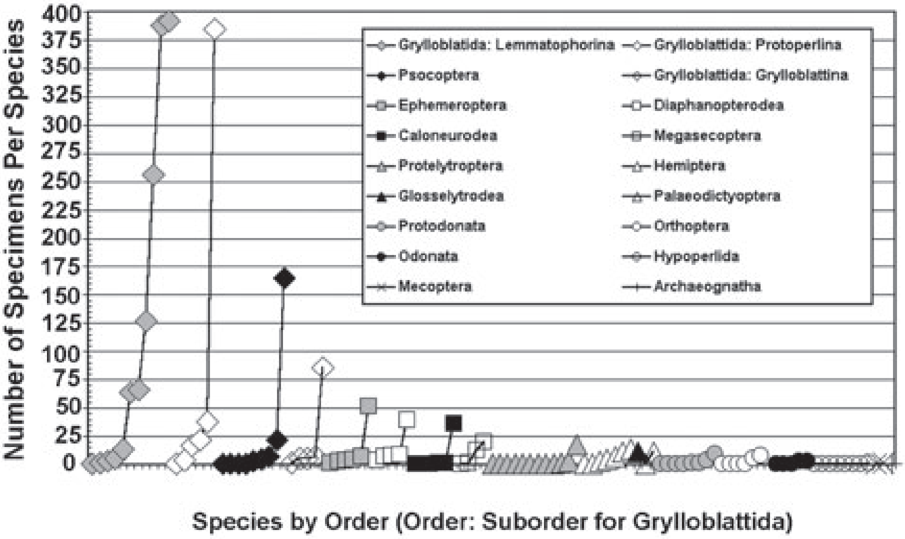

Fig. 13. Adult-specimen abundance distributions of the Elmo entomofauna by major taxonomic groups. Taxa are arranged in order of groups with greatest to lowest species abundance.

Lemmatophora typa, although definitive attribution could not be made. He considered the smaller nymphs most likely to be the species *Lisca minuta* or *Artinska ovata*. The nymphs possessed what appeared to be lateral gills on the first nine abdominal segments, and Carpenter (1935, 1992) stated that the nymphs were aquatic. However, later researchers consider these nymphs to be semi-aquatic (Storozhenko 2002) or even terrestrial (Aristov *et al.* 2006).

At Midco, Carpenter (1979) collected "several hundreds" of specimens of cast nymphal exuviae of Ephemeroptera of the family Protereismatidae. He noted that "Double that number were simply discarded in the field". This would likely make the nymphal protereismatids the most common specimens at Midco. More than 90% of Carpenter's specimens "consist of isolated wing pads from the nymphs and most of the remainder represent a single thoracic segment with the two wing pads attached." He also found several complete or nearly complete specimens. It should be noted that, over the past several years, the authors of this paper have found no similar fossils in collections from the Midco localities, so Carpenter's find may have represented a mass of exuviae washed in from a stream that emptied into the embayment.

Specimen quality

In the initial announcement of his discovery of the Elmo fossil locality, Elias Sellards (1903) noted: "A very large proportion of the wings are complete and their details of structure clear, even the minute hairs often being present." Another measure of quality is the wealth of information known about the morphology of the various insect species making up the entomofauna.

The distribution of species by the body part(s) by which they are known (fore wing, hind wing, wing, fore and hind wings, partially complete insects, and complete insects) is shown in Fig. 14. There are two sets of bars. The left bar in each pair represents the

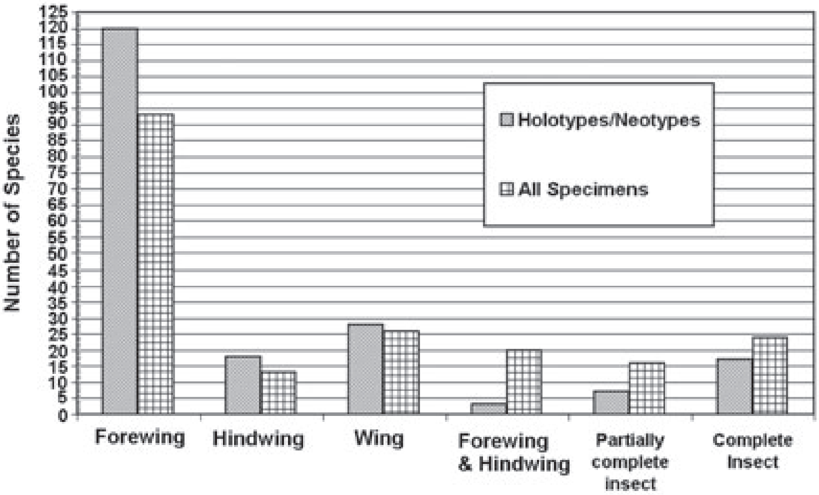

Fig. 14. Distribution of the Wellington Formation species by type of body part(s) for which species are known.

number of species with holotype or neotype specimens that comprise only the mentioned body part. The right bar represents the number of species presently known only by that body part. Thus, for the first pair of bars, representing forewing specimens, we see that 120 species have forewings as holotype or neotype specimens. When all known specimens are considered it becomes evident that hind wings, body parts, or even the complete insect are currently known for some of the taxa that were initially known only by their fore wings. Only 93 species are now known from their forewings alone.

The numbers of species known from various body parts on a percentage basis are compared in Fig. 15. These two charts illustrate the advantage of continued collections and studies of specimens after the species descriptions, and that much more knowledge can potentially be gained about the morphology of these insects.

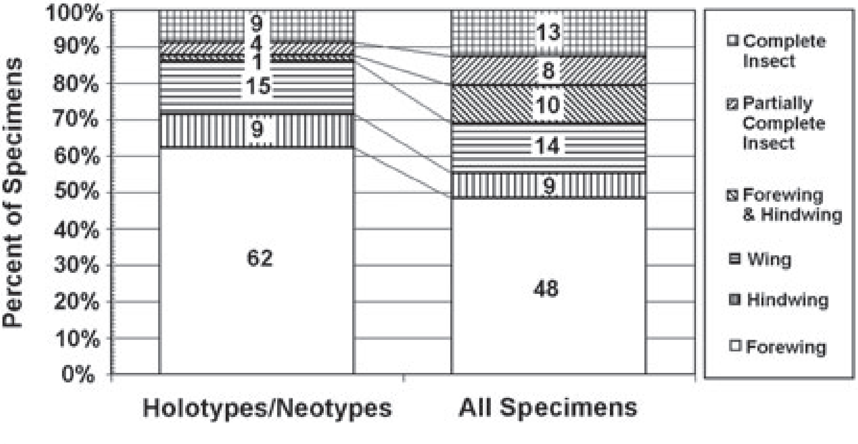

Fig. 15. Relative distribution of the Wellington Formation species by type of body part(s) by which species are known.

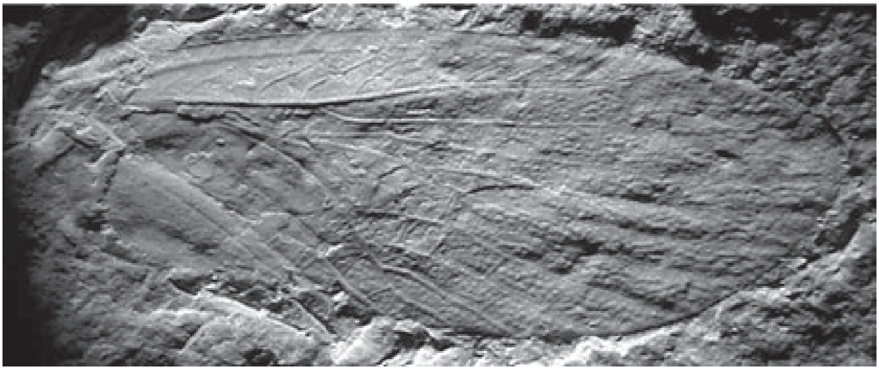

Fig. 16. Fore wing of *Stereopterum rotundum* Carpenter, 1950 (Grylloblattida: Lemmatophorina: Euryptilonidae), collected in March, 2004 from the Midco beds. An example of a species known only from its fore wing.

The authors recently collected a forewing from a locality in Noble County, Oklahoma (Fig. 16). It has been identified as *Stereopterum rotundum* Carpenter, 1950, a grylloblattid species that was described from Elmo. This specimen is the first record of the species from Midco. Just under half of all species from the Wellington Formation are known, as is this species, by fore wings only (Fig. 15).

Another fore wing collected from Noble County (Fig. 17A) represents one of two forewing specimens of *Chelopterum peregrinum* Carpenter, 1950 (Grylloblattida) known to the authors from the Midco, Oklahoma beds. This species also was described from Elmo material. However, additional Elmo specimens allowed Carpenter to reconstruct the entire insect. Based on Carpenter's reconstruction, an original drawing has been made by one of the authors (RJB) (Fig. 17B). As is typical, Carpenter's reconstruction of the insect shows it as if it were pinned in a display case, with its wings extended to illustrate the wing-venation patterns. Another drawing by RJB shows the species as it may have looked in life, with the wings folded over the abdomen (Fig. 17C). As noted in Fig. 15, complete insects are known only for 13% of the Wellington Formation species.

Another measure of the quality of the fossils from the Wellington Formation is what they may reveal about the insects that lived in the Permian. A case in point is the Elmo palaeodictyopteran *Dunbaria fasciipennis* Tillyard in Dunbar & Tillyard, 1924 (Spilapteridae). The species is known from only 10 specimens, but they are of excellent preservation, revealing information on wing colour patterns and morphology of the male and female external genitalia, as well as providing evidence of sexual dimorphism in the hindwing geometry (Kukalová-Peck 1971; Beckemeyer & Byers 2001).

CONCLUSIONS

The Kansas/Oklahoma Wellington Formation has been a major source of information on Lower Permian insect fauna for over 100 years, with nearly 200 species described to date. The Oklahoma beds are poorly known in comparison with the Kansas beds, but both sites meet the criteria for being *Konservat-Lagerstätten*: there is both an exceptional quality and quantity of fossil insect specimens found at these sites.

A number of species of Grylloblattida and one species of Psocoptera seem to be particularly abundant in the Wellington Formation. A study of the paleoecology of the

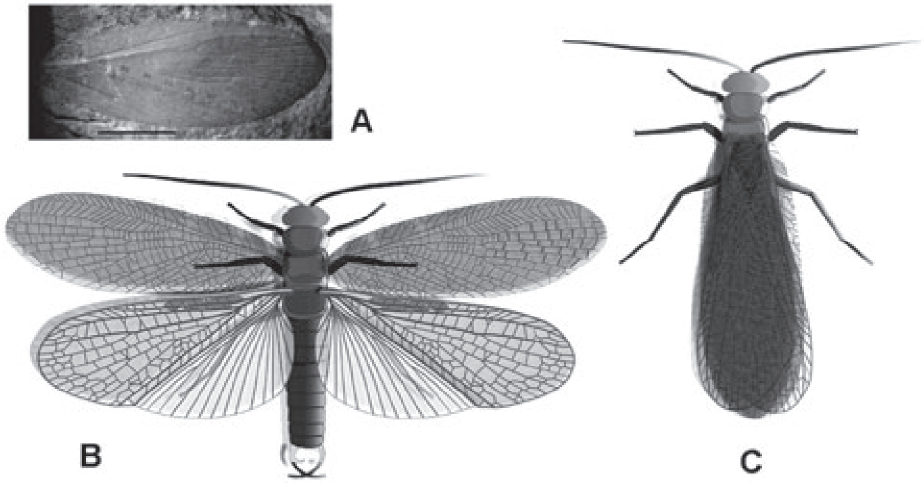

Fig. 17. *Chelopterum peregrinum* Carpenter, 1950 (Grylloblattida: Protoperlina: Chelopteridae), originally described from Elmo: (A) Photograph of fore wing of a specimen collected by the authors from the Midco beds, scale bar 5 mm; (B) Original drawing by Beckemeyer based on reconstruction by Carpenter (1992); (C) Original drawing by Beckemeyer of the insect as it might have appeared in life, with wings folded.

Wellington Permian might determine whether these insects were indeed more abundant or if they have been preferentially preserved, or both.

Large size seems to be a character of the Wellington Formation Protodonata, since 10 of 13 insects with fore wing lengths greater than 50 mm belong to this order. The orders Palaeodictyoptera, Megasecoptera and Caloneurodea each possessed one large species, with most of the Wellington Formation species in these orders being much smaller in size. It may prove beneficial to conduct a similar, complementary, analysis of the Carboniferous fauna, to explore whether there was a greater proportion of large species in these orders at an earlier time.

Much remains to be learned about the Wellington Formation entomofauna, both from unstudied material in current museum collections and from additional fossil material still to be discovered. It is especially important for the Midco Neoptera to be thoroughly reviewed, as there is currently no published, comprehensive survey of the Midco species.

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REFERENCES

Aristov D.S., Novokshonov V.G. & Pan'kov N.N. 2006. Taxonomy of the fossil grylloblattid nymphs (Insecta: Grylloblattida). *Paleontological Journal* **40** (1): 79–89.

Beckemeyer, R.J. 2000. The Permian insect fossils of Elmo, Kansas. *The Kansas School Naturalist* **46** (1): 1–16.

———2004*a*. A new species of †*Martynovia* Tillyard, 1932 (Insecta: †Diaphanopterodea: †Martynoviidae) from the Lower Permian Wellington Formation of Noble County, Oklahoma. *Journal of the Kansas Entomological Society* **77** (2): 127–131.

———2004*b*. A new species of the extinct family †Lophioneuridae from the Lower Permian Wellington Formation of Noble County, Oklahoma. *Journal of the Kansas Entomological Society* **77** (2): 132–136.

———2004*c*. †Raaschiidae (Grylloblattida: †Protperlina), a new insect family from the Lower Permian Wellington Formation of Noble County, Oklahoma. *Journal of the Kansas Entomological Society* **77** (3): 215–221.

Beckemeyer, R.J. & Byers, G.W. 2001. Forewing morphology of *Dunbaria fasciipennis* Tillyard (Palaeodictyoptera: Spilapteridae), with notes on a specimen from the University of Kansas Natural History Museum. *Journal of the Kansas Entomological Society* **74** (4): 221–230.

Béthoux, O., Nel, A. & Lapeyrie, J. 2004. The extinct order Caloneurodea (Insecta: Pterygota: Panorthoptera): wing venation, systematics and phylogenetic relationships. *Annales Zoologici* **54** (2): 289–318.

Carpenter, F.M. 1935. The Lower Permian insects of Kansas. Part 7. The Order Protoperlaria. *Proceedings of the American Academy of Arts and Sciences* **70**: 103–146 + pls 1, 2.

———1939. The Lower Permian insects of Kansas. Part 8. Additional Megasecoptera, Protodonata, Odonata, Homoptera, Psocoptera, Protelytroptera, Plecoptera and Protoperlaria. *Proceedings of the American Academy of Arts and Sciences* **73**: 29–70 + pls 1, 2.

———1947. Lower Permian insects from Oklahoma. Part 1. Introduction and the orders Megasecoptera, Protodonata and Odonata. *Proceedings of the American Academy of Arts and Sciences* **76**: 25–74 + pls 1, 2.

———1950. The Lower Permian insects of Kansas. Part 10. The order Protoperlaria: The family Liomopteridae and its relatives. *Proceedings of the American Academy of Arts and Sciences* **78**: 187–219 + pls 1–3.

———1979. Lower Permian insects from Oklahoma. Part 2. Orders Ephemeroptera and Palaeodictyoptera. *Psyche* **86**: 261–290.

———1992. *Treatise on Invertebrate Palaeontology. Part R. Arthropoda 4. Volumes 3 & 4: Superclass Hexapoda.* Boulder, Colorado and Lawrence, Kansas: Geological Society of America & The Kansas Geological Survey.

Demoulin, G. 1970. Remarques critiques sur des larves "éphéméromorphes" du Permien. *Bulletin de l'Institut royal des sciences naturelles de Belgique* **46** (3): 1–10.

Dunbar, C.O. & Tillyard, R.J. 1924. Kansas Permian insects. Part 1. The geological occurrence and the environment of the insects (Dunbar). With a description of a new palaeodictyopterid (Tillyard). *American Journal of Science (Series 5)* **7**: 171–209 + pls 1, 2.

Engel, M.S. 1998. *Megatypus parvus* spec. nov., a new giant dragonfly from the Lower Permian of Kansas. *Odonatologica* **27**: 361–364.

Grimaldi, D. & Engel, M.S. 2005. *Evolution of the Insects*. New York: Cambridge University Press.

Hall, J.D. 2004. *Depositional Facies and Diagenesis of the Carlton Member (Kansas) and the Midco Member (Oklahoma) of the Wellington Formation (Permian, Sumner Group).* Master's Thesis. Wichita State University, Kansas, USA: Department of Geology.

Hubbard, M.D. & Kukalová-Peck, J. 1980. Permian mayfly nymphs: new taxa and systematic characters. *In*: Flanagan, J.F. & Marshall, K.E., eds, *Advances in Ephemeroptera Biology.* New York: Plenum Press, pp. 19–31.

KLOTS, E.B. 1944. Notes on the Protodonata and Protozygoptera of the Lower Permian of Kansas. *American Museum Novitates* **1260**: 1–7.

KUKALOVÁ-PECK, J. 1968. Permian mayfly nymphs. *Psyche* **75**: 310–327.

———1971. The structure of *Dunbaria* (Palaeodictyoptera). *Psyche* **78**: 306–318.

———1991. Chapter 6. Fossil history and the evolution of hexapod structures. *In*: Naumann, I.D., ed., *The Insects of Austalia, a Textbook for Students and Research Workers.* 2nd Edition. Melbourne, Australia: Melbourne University Press, pp. 141–179.

LUBKIN, S.H. & ENGEL, M.S. 2005. *Permocoleus*, new genus, the first Permian beetle (Coleoptera) from North America. *Annals of the Entomological Society of America* **98** (1): 73–76.

RAASCH, G.O. 1946. *The Wellington Formation in Oklahoma*. PhD Thesis. Madison, Wisconsin, USA: University of Wisconsin.

RASNITSYN, A.P. & QUICKE, D.L.J., eds. 2002. *History of Insects.* Dordrecht *etc.*: Kluwer Academic Publishers.

SELLARDS, E.H. 1903. Discovery of fossil insects in the Permian of Kansas. *American Journal of Science* **16**: 323–324.

STOROZHENKO, S.Yu. 1998. *Systematics, Phylogeny and Evolution of Grylloblattid Insects (Insecta: Grylloblatida)* [*Sistematika, filogenia i evolutsiya grilloblattidovykh nasekomykh (Insecta: Grylloblatida)*]. Vladivostok: Dal'nauka.

———2002. Section 2.2.2.2.1. Order Grylloblattida Walker, 1914 (= Notoptera Crampton, 1915, = Grylloblattodea Brues et Melander, 1932 + Protorthoptera Handlirsch, 1906, = Paraplecoptera Martynov, 1925 + Protoperlaria Tillyard, 1928). *In*: Rasnitsyn, A.P. & Quicke, D.L.J., eds, *History of Insects.* Dordrecht *etc.*: Kluwer Academic Publishers, pp. 278–281.

TASCH, P. 1964. Periodicity in the Wellington Formation of Kansas and Oklahoma. *In*: Merriam, D.F., ed., *Symposium on Cyclic Sedimentation*. Vol. II. *State Geological Survey of Kansas, Bulletin* **169**: 481–496.

TASCH, P. & ZIMMERMAN, J. 1962. The *Asthenohymen-Delopterum* bed – a new Leonardian insect horizon in the Wellington of Kansas and Oklahoma. *Journal of Palaeontology* **36** (6): 1319–1333.